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Subalpine Forest and Scrub in the Tararua Range

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Abstract

THE following types of community are described: *Olearia-Blechnum* scrub on sites between 3,000ft and 4,000ft with well drained, stable soils; *Olearia-Danthonia* stunted scrub on sites where high altitude, exposure or poor drainage preclude tall, dense scrub; scrub communities on steep, exposed, rocky ridges at high altitudes; *Olearia-Polystichum* scrub on sheltered moist sites with unstable substrata; *Griselinia* low forest on sheltered sites below c. 3,800ft with moist, stony, well-drained soils; kamahi low forest below 3,200ft on spurs where the soils are stable, well drained and showing well developed crumb structures; close-canopied silver beech forest on ridges and spurs; silver beech-*Olearia* forest on moist sheltered faces; silver beech-*Danthonia* forest where gales have caused wind-throw on usually sheltered slopes; open canopied silver beech forest on broad, gently sloping ridges; silver beech scrub on high exposed sites.

Though the distribution of most of these communities can be explained satisfactorily in terms of altitude and topography, the scarcity of silver beech in the northern part of the Tararua Range is probably related to the occurrence of frequent dense fogs which descend to low altitudes. Certain anomalies in the regeneration of silver beech and *Dacrydium biforme* are probably to be explained in terms of a warmer climate during the last one hundred years.

INTRODUCTION

THE opportunity to study subalpine vegetation in the Tararua Range arose during the summer of 1958–59 when I took part in a Forest Service survey of the area. The aim of this paper is to describe and classify the communities of subalpine forest and scrub, and to discuss the factors which determine their distribution. Two earlier papers will be referred to frequently; one contains detailed floristic information and a general account of the vegetation (Zotov, Elder, Beddie, Sainsbury and Hodgson, 1938) and the other is a discussion, based mainly on observations in the Tararua Range, about the nature of the vegetation belts and the tree line in New Zealand (Zotov, 1938).

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The Tararua Range is centred on latitude 40° 45′, extends 60 miles in a SSW–NNE direction from Rimutaka Saddle to Manawatu Gorge, and has a maximum width of 18 miles (Text-fig. 1). From Mt. Alpha in the south to near Ruapai in the north there is accordance of major summits, all of which lie between 4,000ft and 5,154ft, but northwards from Ruapai there is a gradual fall in altitudes, and near Manawatu Gorge the hills attain only 1,000ft. Slopes are moderately steep to steep, and the rivers are deeply entrenched in gorges. The heads of a number of valleys, however, have U-forms which suggest that they were sculptured by ice during the Pleistocene (Adkin, 1911). Such valleys, whose floors all lie at about 3,000ft, are referred to in this paper as U-basins. The underlying rock throughout the range is greywacke, and in U-basins there are coarse deposits which seem to be morainic. Subalpine soils range from skeletal types on the steeper and less stable slopes, to alpine gleys where they are most mature. There is widespread accelerated erosion which must be attributed in part to disturbance of the vegetation by introduced browsing mammals, although in certain areas extensive slipping and gullying may have been triggered off by earthquakes.

The prevailing north-west winds, which are often of gale force, have considerable influence on the growth form and distribution of plants in the area. Winds from the south-east are usually less frequent and violent, but on rare occasions they have reached hurricane force and caused heavy damage to forest. Rainfall is heavy throughout the range, the scant records suggesting that it exceeds 150 inches per annum at higher altitudes. Though the eastern flanks undoubtedly receive less rain than the western, there is not sufficient evidence to assume that local differences in rainfall near the tree line are sufficiently great to be of ecological significance. According to Zotov (*et al.*) snow lies for some five months of each year above 4,000ft. There is no precise information about temperature regimes; Zotov's altitudinal belts are based on extrapolations from sea level. Zotov (*et al.*) found that the crests of the Tararua Range are fog-bound for some 200 days a year, and that the lower level of the fogs coincides closely with the tree line. Since these fogs are usually carried in by the north-west winds, the eastern ridges in the vicinity of Mt. Holdsworth are often clear when the remainder of the range is shrouded in fog and drizzle; this is a föhn effect which becomes far more marked at lower altitudes.

The lower slopes of the Tararua Range are completely forested, except marginally where there has been clearance to pasture. South of Mt. Crawford and the Mitre, the tree line of silver beech (*Nothofagus menziesii*) reaches 3,800–4,200ft, and abuts on alpine grasslands. Northwards from here, the extent of silver beech forest becomes progressively smaller, the altitude of the tree line falls, and a broad belt of scrub intervenes between forest and grassland. The lower boundary of the subalpine forest and scrub zone can be regarded as being usually set at 3,000–3,200ft, by *Nothofagus fusca, Fuchsia excorticata, Blechnum discolor* and other species which ascend to about the same level.

Classification and Description of Communities

A. Basis of Classification

Although the subalpine scrub communities of the Tararua Range resemble those described for the Hokitika catchment (Wardle, 1960), especially in the importance of *Olearia colensoi,* floristic differences necessitate a somewhat different classification. In the Tararua Range *Hoheria glabrata* is absent, *Griselinia littoralis* is far more abundant than it is in Hokitika subalpine communities, and *Olearia colensoi* is dominant in three distinct types of community, instead of in only one. Further, in the Tararua Range there are five communities which are characterised by the dominance of silver beech. A list of types of communities follows, together with the abbreviated titles used in the remainder of this paper:

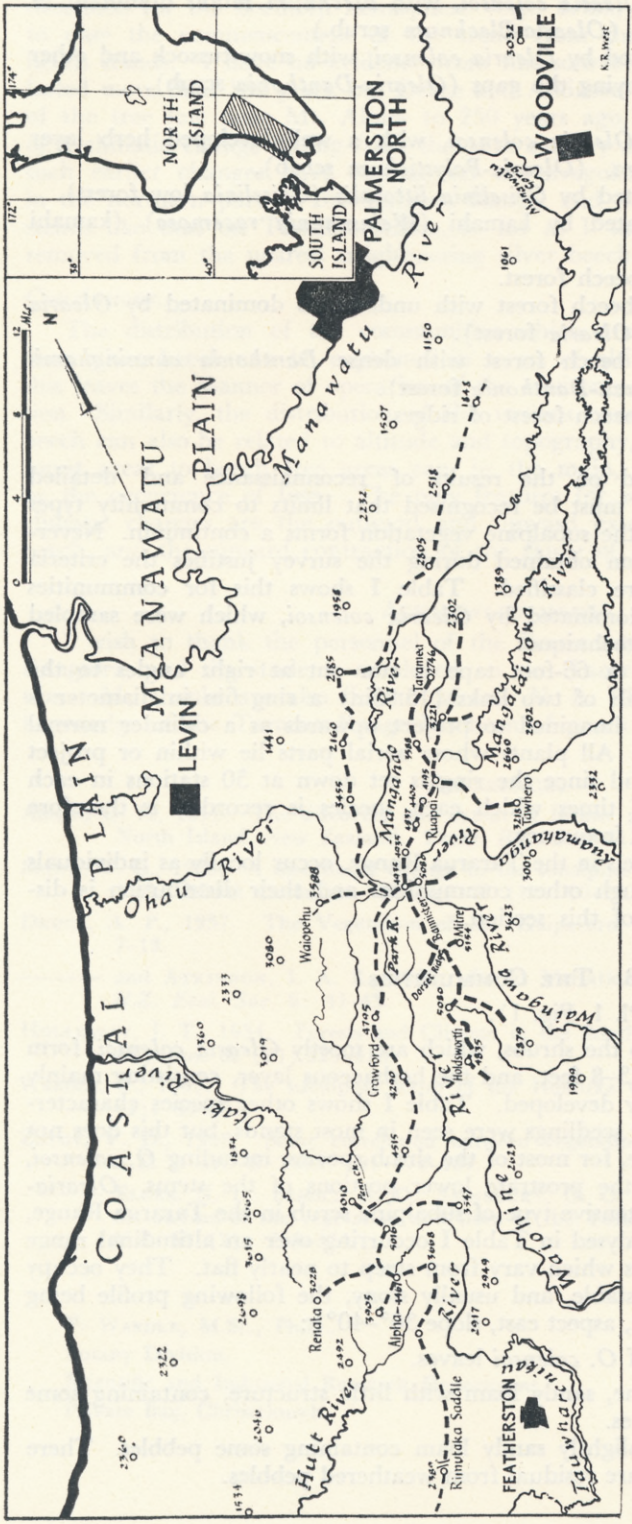

FIG. 1.—Map of the Tararua Range.

Olearia colensoi dominant

Polystichum vestitum and water course

Olearia colensoi dominant

Erosion gutter

Polystichum vestitum dominant

Turf species and water course

Polystichum vestitum dominant

Coprosma ciliata

Group of Olearia lacunosa trees

FIG. 2.—Distribution of Vegetation on a Transect, 80ft long, across Olearia-Polystichum Scrub. To scale.

1. Scrub dominated by *Olearia colensoi,* with *Blechnum minus* dominant in the sparse herb layer. (*Olearia-Blechnum* scrub.)
2. Stunted scrub dominated by *Olearia colensoi,* with snow-tussock and other grassland species occupying the gaps (*Olearia-Danthonia* scrub).
3. High altitude scrub.
4. Scrub dominated by *Olearia colensoi,* with a well-developed herb layer of *Polystichum vestitum.* (*Olearia-Polystichum* scrub).
5. Stunted forest dominated by *Griselinia littoralis* (*Griselinia* low forest).
6. Stunted forest dominated by kamahi (*Weinmannia racemosa*) (kamahi low forest).
7. Close-canopied silver beech forest.
8. Open-canopied silver beech forest with underscrub dominated by *Olearia colensoi* (silver beech-*Olearia* forest).
9. Open-canopied silver beech forest with dense *Danthonia cunninghamii* on the floor (silver beech-*Danthonia* forest).
10. Open-canopied silver beech forest of ridges.
11. Silver beech scrub.

This classification is based on the results of reconnaissance and detailed qualitative description, and it must be recognised that limits to community types can be set only arbitrarily, as the subalpine vegetation forms a continuum. Nevertheless, quantitative information obtained during the survey justifies the criteria by which the communities are classified. Table I shows this for communities representing the three types dominated by *Olearia colensoi,* which were sampled with the following frequency technique:

In a representative stand, a 66-foot tape is run out at right angles to the direction of slope. At intervals of two links (15.85in) a ring 6in in diameter is placed on the ground, and is imagined to project upwards as a cylinder normal to the surface of the ground. All plants whose aerial parts lie within or project into the cylinder are listed, and since the ring is set down at 50 stations in each transect, the total number of times which each species is recorded is therefore equal to half of its percentage frequency.

Podocarps, at subalpine levels in the Tararua Range, occur locally as individuals or small stands scattered through other communities and their distribution is discussed separately at the end of this section.

B. THE COMMUNITIES

1. *Olearia-Blechnum scrub* (Pl. 1, Fig. 1).

In Olearia-Blechnum scrub the shrubs, which are mostly *Olearia colensoi,* form a dense canopy at a height of 3–8 feet, and the herbaceous layer, consisting mainly of *Blechnum minus,* is sparsely developed. Table I shows other species characteristic of this type of scrub. Few seedlings were seen in most stands, but this does not imply an inability to regenerate, for most of the shrub species, including *O. colensoi,* multiply through layering of the prostrate lower portions of the stems. *Olearia-Blechnum* scrub is the most extensive type of subalpine scrub in the Tararua Range, with stands similar to that analysed in Table I occurring over an altitudinal range of 3,000 to 4,000 feet on slopes which vary from steep to nearly flat. They occupy soils which are well drained, stable, and usually stony, the following profile being representative (altitude 3,360ft, aspect east, slope 30°–40°):

Litter, predominantly of *O. colensoi* leaves.

10in of dark brown, fine, sandy loam with little structure, containing some weathering greywacke stones.

8in of greyish brown, slightly sandy loam containing some pebbles. There are reddish mottles which are residual from weathered pebbles.

1. (Upper). *Olearia-Blechnum* scrub 4ft tall in foreground, passing into *Olearia-Danthonia* scrub on gentler slope. 3,600ft.
2. (Middle). Snow-tussock on gentle slopes, scrub 5–8 feet tall of *Olearia colensoi* and *Dracophyllum filifolium* on steeper slopes. 3,400–3,500 feet.
3. (Lower). Silver beech extends from the crest of a spur onto the lee slope (out of sight). Most of the windward, north-west facing aspect is occupied by grassland. 3,900–4,000 feet, in eastern part of the Tararua Range.

1. (Upper left). Poorly drained ground is occupied by broad-leaved snow-tussock accompanied by *Olearia colensoi*, which is stunted to 6in tall. 3,600ft.
2. (Lower left). Silver beech-*Danthonia* forest with dead *Olearia colensoi*. 3,700ft.
3. (Upper right). Tree line of silver beech falls from 3,800ft to 3,000ft at the lip of the U-basin forming the head of South Mitre Creek. Marginal beech trees are wind pruned. Most of *Olearia colensoi* is dead, living "scrub" is mainly *Griselinia* low forest.
4. (Lower right). In the head of Tauwharenikau River, silver beech begins where the gradient of the valley steepens and its width decreases.

TABLE I.—Percentage Frequency of Species in Three Communities Dominated by *Olearia colensoi*.

	Olearia-Blechnum	*Olearia-Danthonia*	*Olearia-Polystichum*
Shrub species			
Olearia colensoi	80	86	32
Nothopanax sinclairii	20		
Coprosma foetidissima	20		
Olearia lacunosa			18
Coprosma pseudocuneata	16	2	8
Dracophyllum filifolium	14		
Senecio elaeagnifolius	6		
Hebe evenosa			6
Dracophyllum uniflorum		6	
Nothopanax colensoi	4		2
Coprosma ciliata			4
Pimelea gnidia		4	
Myrsine divaricata	2		
Coprosma colensoi	2		
Herbaceous species			
Polystichum vestitum			56
"Broad-leaved snow-tussock"		54	
Blechnum minus	46	8	
Astelia cockaynei	36	2	
Epilobium sp.			32
Poa breviglumis			26
Danthonia cunninghamii			24
Cardamine heterophylla			12
Viola filicaulis			10
Uncinia sp.	2	2	8
Gentiana sp.		8	
Hymenophyllaceae spp.	6	2	
Phormium colensoi	2		6
Ranunculus hirtus			6
Pratia angulata			6
Hydrocotyle sp.			4
Scirpus sp.			2
Euphrasia cuneata			2
Senecio solanderi			2
Graminiae sp.			2
Grammitis billardieri	2		
Carex sp.		2	
Bulbinella hookeri		2	
Aciphylla dissecta		2	
Poa colensoi		2	
Unidentified			2
% Frequency of living shrubs	98	88	60
% Frequency of herbaceous spp.	48	62	94
% Frequency of vascular plants	100	98	100

Along gradients of increasing altitude, exposure, stoniness or instability of soil, and decreasing drainage, we find transitions towards other scrub types. The taller species such as *Senecio elaeagnifolius* and *Nothopanax sinclairii* increase as exposure and altitude decrease, until there is a gradual transition into kamahi low forest. *Dracophyllum filifolium*, which has relatively light-demanding seedlings, increases in importance on drier sites such as ridges and northerly aspects, and often becomes co-dominant.

2. *Olearia-Danthonia scrub* (Pl. 1, Figs. 1 and 2; Pl. 2, Fig. 1).

With increasing altitude and exposure the canopy of *Olearia-Blechnum* scrub becomes lower and less continuous, and gaps appear which are occupied by snow-tussock (large species of *Danthonia*) and by other grassland species. It is usually the broader-leaved of the two Tararua forms of snow-tussock which is associated with *Olearia colensoi*. *O. colensoi* occurs as high as 4,750ft on sheltered slopes where rockiness of the ground has reduced competition from snowgrass, and, stunted to a height of 6–12in, it is often present in poorly drained alpine grassland where snow-tussock shares dominance with turf forming species such as *Carpha alpina*. Finally, in the mosaics and mixtures of tall scrub and grassland which may descend to as low as 2,500ft on gentle slopes, *O. colensoi* either dominates the scrub component or shares dominance with *Dracophyllum filifolium*.

3. *High altitude scrub.*

On steep, exposed, rocky ridges and spurs the continuity of the high altitude grassland is broken and hardy shrubs, especially *Dracophyllum uniflorum* and *Senecio bidwillii*, may be dominant over small areas. Such high altitude scrub is always fragmentary and covers only a small total area, although its range extends from 4,000ft to the highest summits. There is every gradation to the rock communities of herbs and cushion plants which occupy the most severe habitats. Below 4,000ft steep rocky slopes provide less severe habitats, so that low-growing *Olearia colensoi* becomes dominant and *D. uniflorum* and *S. bidwillii* become only minor components.

4. *Olearia-Polystichum scrub.*

In *Olearia-Polystichum* scrub *Olearia colensoi*, growing up to 8 feet tall, is the dominant shrub, and *Polystichum vestitum* dominates the dense herb layer. Other common shrubs include *Senecio elaeagnifolius, Coprosma pseudocuneata, C. foetidissima, Aristotelia fruticosa* var. *suberecta, Nothopanax sinclairii* and *Myrsine divaricata*. Typical stands were seen over an altitudinal range of 3,500ft to 4,100 feet. They occupy relatively sheltered sites where the soils are moist, well-drained, loose, stony, sandy loams derived from scarcely stabilised talus or fault-shattered greywacke. Because of the instability of the substratum, the vegetation consists of strips of communities in different stages of development (see Text-fig. 2); such species as *Epilobium* sp., *Poa breviglumis, Cardamine heterophylla* and *Danthonia cunninghamii* are characteristic of the earlier, more open stages. That there is a relationship between *Olearia-Polystichum* scrub and *Griselinia* low forest is indicated by scattered trees and groves of *Griselinia littoralis, Olearia lacunosa, O. ilicifolia* and the subalpine form of *Hoheria sexstylosa*.

5. *Griselinia low forest.*

Griselinia low forest is distinguished by the dominance of *Griselinia littoralis*, growing to as tall as 30 feet. *Olearia lacunosa* and *Hoheria sexstylosa* are commonly associated trees, while *Podocarpus hallii* and *Olearia ilicifolia* occur more locally. *Olearia colensoi, Senecio elaeagnifolius, Myrsine divaricata, Coprosma parviflora, C. ciliata, C. pseudocuneata, C. foetidissima, Nothopanax sinclairii* and *Pseudowintera colorata* grow in the shrub storey. The herbaceous stories have been greatly modified by browsing animals; species now present include *Polystichum vestitum, Danthonia cunninghamii, Ranunculus hirtus, Hydrocotyle* sp., *Viola filicaulis* and *Phormium colensoi*.

Griselinia low forest grows on relatively sheltered sites with stony but stable, moist, well-drained soils, and is especially characteristic of the U-basins, where it appears as bright green fingers which extend along the watercourses through the general grey-green scrub dominated by *Olearia colensoi*. *Griselinia littoralis* reaches 3,800ft, but most of the associated trees fall out below this altitude. *Olearia*

lacunosa, however, extends to higher altitudes (over 4,000ft) and to drier sites. Below 3,200–3,000ft *Griselinia* low forest grades into related communities enriched by such species as *Fuchsia excorticata, Schefflera digitata, Carpodetus serratus* and *Cordyline indivisa*, while the subalpine species (notably the three *Olearia* spp. and *Senecio elaeagnifolius*) drop out.

6. *Kamahi low forest*

Kamahi is dominant in most of the forest areas where *Nothofagus* spp. are absent. At lower altitudes there is a wealth of associated species, but above 2,500–2,800 feet most of these drop out, and towards the upper limit of kamahi the main accompanying species are *Podocarpus hallii, Pseudowintera colorata, Blechnum discolor* and *Cyathea colensoi*. Kamahi itself develops a characteristic, close, windshorn canopy near its upper limit, where it may be stunted to a height of 6ft. Such low forest grows on spurs where the soils are well-drained and show well-developed crumb structures. Kamahi low forest meets either *Olearia-Blechnum* scrub or mixtures of scrub and grassland, the boundary being sharp where it coincides with a change of slope, but otherwise taking the form of a broad ecotone where the two communities form a mosaic. The forest usually ascends to 3,000–3,200 feet, but on flatter, more exposed areas subalpine scrub communities descend to below 2,000 feet.

7. *Close-canopied silver beech forest*

On drier sites such as ridges and spurs, silver beech forest usually has a close canopy with few gaps, so that lower stories are poorly developed. When exposed to frequent and violent winds, the canopy is low (20–30 feet), wind-shorn and especially dense, and the forest interior is dark. In such communities on the western side of the Tararua Range a thick cover of mosses, *Hymenophyllaceae* and lichens clothes tree trunks, fallen logs and projecting rocks and tree roots, while the forest floor has a thick litter of beech leaves, scattered tufts of a small *Uncinia* sp., and scattered suppressed seedlings of silver beech and *Olearia colensoi*. Under the less humid climate of the eastern part of the range development of the mossy cover is slight. In less exposed situations, silver beech is taller, its canopy is less dense, and seedlings of silver beech are common, although usually heavily browsed by deer. The lower stories are still poorly developed, but this also may be an effect of deer.

8. *Silver beech–Olearia forest*

On moist, relatively sheltered faces the silver beech storey consists of well-spaced large trees, up to 30in in diameter and over 40ft tall, so that the forest interior receives sufficient light for the development of a dense scrub understorey dominated by *Olearia colensoi. Polystichum vestitum* and *Danthonia cunninghamii* are abundant, indicating a relationship to *Olearia-Polystichum* scrub, while below 3,700–3,600 feet *Griselinia littoralis, Hoheria sexstylosa* and *Olearia lacunosa* —species typical of *Griselinia* low forest—enter the stands. Below 3,200 feet such species as *Fuchsia excorticata* and *Carpodetus serratus* begin to replace the subalpine species. Though seedlings of shrubs, especially of *Olearia colensoi*, are abundant, silver beech seedlings occur only sparsely, and most of them are perched on logs and on the trunks of living silver beech trees.

Silver beech increases in density on drier and more exposed slopes, as the stands approach the close-canopied type, whereas it drops out towards steep gullies with young, unstable soils, leaving us with *Olearia-Polystichum* scrub.

9. *Silver Beech-Danthonia forest* (Pl. 2, Fig. 2).

Over large areas in the central and southern parts of the range relatively sheltered slopes which might be expected to carry silver beech-*Olearia* forest or taller, less dense variants of close-canopied silver beech forest actually carry a

rather different type of community. Mainly as a result of the south-easterly gale of February 2, 1936, but perhaps also in part a result of other storms, the silver beech canopy has been opened up and there are numerous fallen logs. Nearly all the windthrown areas are on usually sheltered eastern aspects; on western aspects which are exposed to the prevailing winds, the trees are adapted to withstand frequent gales. This damaged forest has a dense understorey formed by the large tussocks of *Danthonia cunninghamii*. There are scattered shrubs and small trees of species characteristic of silver beech-*Olearia* forest, but like the silver beech itself they show little effective regeneration, because of browsing by deer. (*D. cunninghamii* is dominant also over two areas where fire has destroyed the original silver beech forest).

10. *Open-canopied silver beech forest on ridges*

On broad, gently-sloping ridges at 3,900 feet, at Dorset Ridge and one mile east of Mt. Alpha, there is silver beech forest characterised by the presence of open glades. The trees form a windswept canopy at 25–30 feet, and *Olearia lacunosa, O. colensoi, Coprosma pseudocuneata* and *Myrsine divaricata* are present. The glades are occupied by a browse-induced turf of *Poa breviglumis, Carex* sp. and other herbs, while species of *Hymenophyllaceae* occur under the trees. In the South Island similar stands are characterised by heavy accumulation of winter snow.

11. *Silver beech scrub*

In high exposed places silver beech is often reduced to a shrub form, and then it shares dominance with such species as *Dracophyllum filifolium* and *Olearia colensoi*. This scrub merges into grassland with increasing exposure.

C. DISTRIBUTION OF PODOCARP SPECIES

Dacrydium biforme is mainly confined to the area north-east of the ridge crests joining Taramea, Ruapai and Tawhero, but there are isolated occurrences elsewhere in the northern part of the Tararua Range. It is virtually restricted to the crests of ridges and spurs, where it is associated with *Olearia-Blechnum* scrub, with communities transitional between *Olearia–Blechnum* scrub and kamahi low forest, and sometimes with snow-tussock grassland. On slopes of less than 10° *D. biforme* forms dense groves, almost to the exclusion of other species, but on steeper slopes it usually ocurs only as scattered trees. Although *D. biforme* trees are usually not more than 15 feet tall, they attain diameters of up to 30in. *D. biforme* occurs between the altitudes of 2,000 and 3,700 feet, on soils which are clay loams with difficult drainage. These soils are often alpine gleys like the following example from scrub dominated by *Olearia colensoi,* growing on the crest of a spur at an altitude of 3,300 feet and on a slope of 10°.

Litter of *O. colensoi*, snow-tussock and *D. biforme.*
2in of dark brown, fine-sandy loam. Gradual transition to
8in of greyish brown, structureless, clay loam, containing most of the roots. Gradual transition to
8–10in of brownish grey, compact clay loam. Dark brown mottling due to humus, and also reddish mottling, especially in the top 2in of the horizon.
Abrupt change to undulating iron pan, consisting of:
$\frac{1}{16}$in of dark reddish brown layer, cemented hard.
$\frac{1}{4}$in of orange layer, gradually passing to
1in of ochre layer, and gradual transition to
4in light yellowish-brown clay loam, with crumb structure and containing small rock fragments.
Solid greywacke.

Phyllocladus alpinus occurs over the same range of habitats as *Dacrydium biforme,* but it is distributed throughout the portion of the range north of the head of the Otaki River and Mt. Bannister, and other isolated stands have been reported. Usually it forms suppressed, layering growth, but it can become a small tree and is occasionally dominant.

Podocarpus hallii occurs throughout the Tararua Range and, though not common at higher altitudes where silver beech is present, it is always present in kamahi forest, and is sometimes found in *Griselinia* low forest and in lower altitude, less exposed *Olearia–Blechnum* and *Olearia–Danthonia* communities. In scrub communities, where it reaches 3,500 feet, *P. hallii* is usually stunted to a shrub less than 3 feet tall.

Podocarpus nivalis grows in several localities in the northern part of the range. In the basin north of Mt. Bannister, *P. nivalis* and *P. hallii* are both present, together with distinctly intermediate forms.

Discussion

When attempting to rationalize the plant geography of an area, it is logical to relate the distribution of the plants, so far as possible, to the existing environmental factors. But it may be found that there is a residue of features which is difficult to explain in this way, in which case it may be necessary to postulate past or current changes in some of the environmental factors—e.g., changes in climate, or changes in the biota through immigration or introduction. Such is the position in the Tararua Range, and the following discussion accordingly falls into two parts.

A. Distribution of Subalpine Vegetation in Relationship to the Present Environment

Distribution of subalpine scrub communities, from which silver beech is absent.

Above 4,000 feet grassland is the most extensive vegetation, but it includes scattered shrubs (of *Olearia colensoi, Senecio bidwillii, Dracophyllum uniflorum* and *Hebe astoni*) whose abundance increases with increasing steepness and where the tussock cover is broken because of stoniness or poor drainage. Whereas the species of the high altitude scrub congregate on exposed rocky spurs, *O. colensoi* increases on more sheltered steep faces and in shallow gullies. Exposure to wind reduces the size and density of *O. colensoi* and favours snow-tussock, so that ridge crests often sharply divide snow-tussock on the windward side from *O. colensoi* on the lee; this may well be an indirect effect, through the influence of wind on the distribution of the snow cover. The altitudinal limit of *O. colensoi* may be determined by the winter climate, for I observed that many plants at higher altitudes had dried-up terminal buds which had failed to open in the spring and shoots with small malformed leaves. This damage must have been caused during the preceding winter, when the unusually light snow fall left the shoots unprotected from low temperatures and desiccating winds. *Dracophyllum uniflorum, Senecio bidwillii* and *Hebe astoni* ascend to the highest summits, and thus do not reach the limits of their cold tolerance.

Below 4,000 feet scrub becomes increasingly extensive and vigorous. Snow-tussock descends to low altitudes, however, on broad, gently sloping spurs and ridges; in the northern part of the range it descends to as low as 2,500 feet. At such places thickets of scrub occupy knolls, hollows and steeper ground, whereas on flatter ground there are mixtures of shrubs and grassland species. This pattern may be related to soil factors. In the grassy areas there are usually 12–15in of compact, weak-structured silt loam or clay loam above the first weathering greywacke stones, the profile being that of an alpine gley, with iron and humus pans

developed at 15–20in and blue reducing horizons at 10–12in. The soils of steeper, scrub-covered slopes are less compact, and contain weathering stones almost to the surface. As Druce (1957) notes, poor drainage of the grassy areas is indicated by the presence of such species as *Carpha alpina.*

At still lower altitudes, though not in areas where silver beech is present, subalpine scrub in turn replaces forest on gently sloping ridges and spurs, especially in the northern part of the range where scrub dominated by *Olearia colensoi* descends to 1,600 feet at Baber's Saddle (Zotov *et al.*). In such communities *Phyllocladus alpinus, Podocarpus hallii* and, in the north-eastern part, *Dacrydium biforme* are present. The soils are again alpine gleys, which contrast with the well-drained soils of the forested slopes below.

Grassland replaces scrub also on the floors of the U-valleys forming the heads of the Park and Waiohine Rivers, at about 3,000 feet. I do not agree with the suggestion of Zotov (*et al.*) that these grassy bottoms are related to a drier climate. Like the deep fault trenches along the ridges, which have snow-tussock on their floors and scrub on their walls, they are typical frost hollows, though soil type, drainage and duration of snow cover may also be involved. The dominance of the narrow-leaved snow-tussock is significant, for this form predominates also at the highest altitudes.

It is therefore not likely that the relative distribution of scrub, grassland, and forest is everywhere determined by the same set of factors. Factors related to drainage and development of soil may well be responsible for the pattern of communities on gentle slopes; there are other patterns which are more likely to be due to temperature effects or exposure to wind.

Distribution of silver beech where it forms a continuous subalpine forest.

The spurs and ridges of the southern part of the Tararua Range are mainly occupied by close-canopied silver beech forest. Towards gullies and moist faces the height and girth of the beech trees increase, but their density decreases, because the dense understories of subalpine shrubs or *Danthonia cunninghamii* cause regeneration of the relatively light-demanding beech to be sporadic.

Silver beech reaches its maximum altitude on spurs and ridges at about 3,800 feet in the west and 4,200 feet in the east, near Mt. Holdsworth, where the higher tree line may be related to less frequent fogs and a consequent warmer growing season. As Zotov points out, wind force does not as a rule affect the altitude of the tree line, and stunted prostrate beech on the windward side of a ridge usually reaches the same altitude as tree-form beech on the lee. Near Mt. Holdsworth, however, there are examples of spurs with snow-tussock clad windward, western slopes and forested lee slopes with wind-shorn beech extending right to their crests (Plate 1, Fig. 3). Probably desiccation in this area is stronger than elsewhere in the range, due to the föhn effect.

The altitudes of silver beech tree lines fall slightly in passing from spurs to gullies. They fall further in the heads of larger valleys, and in U-basins the fall of the tree line is very marked indeed. (Pl. 2, Figs. 3 and 4). For example, in South Mitre Creek the steep sides of the V-shaped valley are clothed with forest, silver beech forming the tree line at 3,800 feet, but at the point where the narrow valley abruptly passes into the U-shaped upper basin, the limit line of the silver beech drops sharply to 3,000 feet. The vegetation in this basin is mainly scrub dominated by *Olearia colensoi* and *Griselinia* low forest, and though there are a few clumps of silver beech, they occur only within 500 feet of the margin of the beech forest. This pattern is repeated throughout the southern part of the range, and with variations throughout the South Island mountains, too. Though the factors causing the pattern have yet to be determined, it is suggested on the strength of current investigations in the Canterbury mountains that the growing season in U-basins is either too cool or too short for the growth of silver beech.

Distribution of silver beech where it forms an irregular or discontinuous forest.

As one approaches the northern part of the Tararua Range the beech tree line falls and becomes very irregular, leaving islands of beech well above the general tree line. Islands of silver beech also occur where there is no continuous forest of silver beech at all, for example in the head of the Otaki River and in Penn Creek, where some isolated clumps are at least a quarter of a mile from the nearest neighbouring silver beech. They are always sited on spurs, thus confirming that the species demands good insolation.

In order to explain the discontinuous distribution of silver beech in the Tararua Range it is necessary to postulate a north-south environmental gradient which is related in some way to the position of Manawatu Gorge, for the distribution of subalpine beech in the Ruahine Range (in this case *Nothofagus cliffortioides*) is a mirror image of that in the Tararua Range (Elder* in litt.). The smaller area in Penn Creek where silver beech forest is discontinuous can in much the same way be related to the valley of the lower part of the Otaki River. Zotov (*et al.*) state that silver beech does not occur above the lower altitudinal limit of heavy fogs, and infer that in the northern part of the range the fogs descend so low that silver beech is excluded from subalpine levels. Such a negative relationship between subalpine beech forest and frequent fogs appears to hold also for other parts of New Zealand. Zotov (*et al.*) suggest that fogs reduce the light intensity so drastically that beech seedlings cannot compete with those of *Olearia colensoi,* but it would be desirable to re-investigate this point in view of subsequent improvements in the techniques of light measurements in the field.

B. Past and Present Changes in Environmental Factors

Effect of introduced herbivores

The influences of deer and opossums on the vegetation in the Tararua Range are profound, but since they are discussed fully in a bulletin of the New Zealand Forest Service (publication pending) they will be passed over in the present discussion. This paper is substantially an account of the primeval subalpine vegetation as it was prior to the introduction of browsing mammals; only one of the community types described—i.e., silver beech–*Danthonia* forest, appears to owe much of its character to browsing influences.

Evidence for climatic change.

There has been much interest in the effects of climatic changes on vegetation since the publication of Holloway's "Forests and Climates of the South Island of New Zealand" (1954). Holloway postulates that since the 14th century A.D., the climate of the South Island has become cooler and drier. If similar climatic changes have affected the Tararua Range, there should be evidence of this in the subalpine vegetation. To find such evidence it is necessary to look for anomalies in the regeneration patterns of the longest-lived trees—i.e., silver beech and *Dacrydium biforme,* whose respective life spans are probably over 500 and 1,000 years, and also *Podocarpus hallii.* Anomalies in regeneration patterns of the shorter-lived species can be explained in terms of succession, browsing, epidemics and vegetative reproduction.

In the case of silver beech, dearth of effective regeneration was noted in many stands, but usually this could be confidently ascribed to browsing by deer. On the other hand, in many instances if not generally, silver beech shows an unmistakable tendency to advance into adjoining subalpine scrub and grassland. Usually the zone of advance, marked by seedlings, saplings and young trees, is only a few

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yards wide, but towards the northern part of the range, where the subalpine silver beech forest is broken into discontinuous fragments, saplings in subalpine scrub are up to 300 feet distant from parent trees. Zotov makes the following comment:

"In the areas subject to fog the timber-line follows a tortuous course, with isolated groups of trees often standing up to 50 m above the main forest. Everywhere along the timber-line the competition is easy to observe. *Nothofagus* seedlings are numerous for about 10 m distance on either side of the line, though seldom any but those immediately above the line are able to lift their crowns above the surrounding plants. Thus the timber-line gradually advances. As a rule, however, there is not sufficient regeneration taking place in the rear and, as the old trees begin to die, all available light is at once monopolised by *Olearia colensoi* and other scrub species. It often happens that in this way portions of the forest many hectares in extent are cut off in the rear from the main body."

Zotov's account implies that waves of regenerating and degenerating silver beech continually proceed up-hill. I find this difficult to accept, and it seems more likely that the invasion of scrub by beech should lead eventually to stands of the silver beech–*Olearia* type. In such stands there is indeed a paucity of silver beech seedlings and saplings, but this is probably offset by the following processes, which appear to lead to effective regeneration, or at least to rejuvenation of old trees:

1. Layering of shoots.
2. Sucker shoots arising from the bases of major roots after trees have fallen over.
3. Adventitious roots arising on the main trunk, sometimes 6–10 feet above the ground which they grow down to meet. This feature is usually found in old degenerate trees whose trunks are heavily overgrown with moss.
4. Epiphytic seedlings perched on old trees succeeding in sending roots to the ground.

Populations of *Dacrydium biforme* associated with *Olearia–Blechnum* scrub on less well drained sites are regenerating freely, but on the steeper slopes below 3,000 feet where kamahi is important, the populations are almost entirely composed of mature trees. This suggests that the territory of *D. biforme* is contracting.

There are numerous stumps and standing dead trunks of *Podocarpus hallii* and also a few dwarfed surviving trees at 3,400 feet in a basin north of Mt. Bannister, above the junction of subalpine scrub with kamahi low forest. Seedlings are abundant, and have a straggling form which suggests some genetic influence of *P. nivalis,* but no plants of intermediate size were noted. This is the only example which I saw in the Tararua Range of a clear age gap in the population of a subalpine tree. Though the situation is parallel to that described for *Libocedrus bidwillii* in the Hokitika catchment (Wardle, 1960), before it can be accepted as evidence for a climatic change it will be necessary to re-examine the area for evidence of fire or other catastrophies.

Acceptable botanical evidence for recent climatic change in the Tararua Range reduces to the advance of silver beech into subalpine scrub and grassland, and the contraction of the territory of *Dacrydium biforme.* Since subalpine scrub appears to be characteristic of areas which do not receive enough warmth and light to allow the growth of silver beech and *D. biforme* is favoured by poor drainage and high frequency of fog, it is likely that the direction of the change has been towards a warmer and sunnier climate. This is in line with the well-documented retreat of glaciers in both hemispheres, and with the forest advances

described for the northern hemisphere (e.g., Brink, 1959). It should be possible to date the commencement of the trend from the age structure of advancing beech stands. I have no evidence from this source to indicate that the trend has lasted more than 100 years, but Druce and Atkinson (1959) date a small extension of the tree line near Mt. Alpha to 250 years ago. Although no clear evidence of a climatic change dating from the 14th century A.D. was found, it is likely that such earlier changes have bearing on the irregular distribution of silver beech in the northern part of the Tararua Range, and particularly on the isolation of stands like that on Tawhero which, as far as I know, is more than two miles removed from the nearest neighbouring silver beech.

Conclusions.

The distribution of the communities which are dominated by species other than silver beech can be explained in terms of altitude and topography, though this leaves the manner of operation of the environmental factors as an open question. Similarly, the distribution of the various communities dominated by silver beech can also be related to altitude and topography, but the relationship of beech forest areas to beech free areas can, in the main, only be tentatively explained by the occurrence of fogs. The only features for which it is useful to postulate climatic changes are the outward and upward extension of the range of silver beech, and the upward contraction of the range of *Dacrydium biforme*.

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